

<https://helda.helsinki.fi>

Understanding the Venus flytrap through mathematical modelling

Lehtinen, Sami

2018-05-07

Lehtinen , S 2018 , ' Understanding the Venus flytrap through mathematical modelling ' ,
Journal of Theoretical Biology , vol. 444 , pp. 1-10 . <https://doi.org/10.1016/j.jtbi.2018.02.003>

<http://hdl.handle.net/10138/233534>

<https://doi.org/10.1016/j.jtbi.2018.02.003>

cc_by

publishedVersion

Downloaded from Helda, University of Helsinki institutional repository.

This is an electronic reprint of the original article.

This reprint may differ from the original in pagination and typographic detail.

Please cite the original version.



Understanding the Venus flytrap through mathematical modelling

Sami Lehtinen

Department of Mathematics and Statistics, FI-00014 University of Helsinki, Finland



ARTICLE INFO

Article history:

Received 5 November 2017

Revised 29 January 2018

Accepted 3 February 2018

Available online 6 February 2018

Keywords:

Carnivorous plants

Cost-benefit model

Beddington–DeAngelis functional response

ABSTRACT

Among carnivorous plants, the Venus flytrap is of particular interest for the rapid movement of its snap-traps and hypothesised prey selection, where small prey are allowed to escape from the traps. In this paper, we provide the first mathematical cost-benefit model for carnivory in the Venus flytrap. Specifically, we analyse the dynamics of prey capture; the costs and benefits of capturing and digesting its prey; and optimisation of trap size and prey selection. We fit the model to available data, making predictions regarding trap behaviour. In particular, we predict that non-prey sources, such as raindrops or wind, cause a large proportion of trap closures; only few trap closures result in a meal; most of the captured prey are allowed to escape; the closure mechanism of a trap is triggered about once every two days; and a trap has to wait more than a month for a meal. We also find that prey capture of traps of the Venus flytrap follows the Beddington–DeAngelis functional response. These predictions indicate that the Venus flytrap is highly selective in its prey capture.

© 2018 The Author(s). Published by Elsevier Ltd.

This is an open access article under the CC BY license. (<http://creativecommons.org/licenses/by/4.0/>)

1. Introduction

The Venus flytrap (*Dionaea muscipula*) is a carnivorous plant, which captures insects in a snap-trap in one of the fastest movements that has been observed in the plant kingdom. This plant, with its unique trapping mechanism, has drawn great scientific interest ever since Darwin (1875), who performed a number of detailed experiments on the plant and called it “one of the most wonderful in the world”. However, it was only recently that the mechanism of the snap-trap closure was fully understood (Forterre et al., 2005; Volkov et al., 2008). By and large, the scientific papers about the Venus flytrap focus on its physiological aspects, whereas few studies have focused on its ecology. As far as the author is aware, trap closures have not been adequately studied in the plant’s endemic habitat. Consequently, there is little information about prey escapes, and even less about hypothesised prey selection, where the trap allows small prey to escape (Darwin, 1875; Gibson and Waller, 2009; Hutchens and Luken, 2009). The costs and benefits of carnivory in the Venus flytrap are generally understood as a trade-off between investments in snap-trap structures and energetic benefits associated with carnivory (Givnish et al., 1984; Ellison and Gotelli, 2001, 2009; Kruse et al., 2014; Pavlovič and Saganová, 2015). However, mathematical cost-benefit models have long been lacking. Thus, as we believe, a robust model for

the costs and benefits of carnivory in the Venus flytrap has to be formulated in order to better understand the ecology of the plant.

The structure of the plant is well known, and for detailed descriptions of it we refer to Darwin (1875, pp. 286–320) and Lloyd (1942, pp. 177–212). The process in which the Venus flytrap captures and digests prey with the snap-traps can be divided into three states, that have been illustrated in Fig. 1. Firstly, a trap is open, and the lobes stand at approximately right angle to each other. In this position the trap remains waiting for a prey to enter it. When a prey eventually shows up and moves across the surface of the trap, it is likely to stimulate one of the trigger hairs. The mechanical stimuli generates a receptor potential followed by an action potential (Hodick and Sievers, 1989; Forterre et al., 2005; Volkov et al., 2008). Under the ordinary conditions of the Venus flytrap, it takes two mechanical stimuli within a thirty second period to cause a signal for trap closure, but at higher temperatures even just one stimuli may suffice (Brown and Sharp, 1910). The observations by Williams (1980) suggest that also raindrops or wind can cause the trap to close, but the frequency of these false alarms is largely unknown.

Secondly, immediately following the signal for closure, the trap snaps shut in a mere second and enters a semi-closed state. The trap remains semi-closed waiting for further mechanical stimuli to ensure that it has caught a living prey. The two lobes are held together, but not tightly, which leaves a window of escape for the caught prey. Darwin (1875, p. 312) conjectured that the Venus flytrap deliberately allows all small prey with little nutriment to es-

E-mail address: sami.lehtinen@helsinki.fi

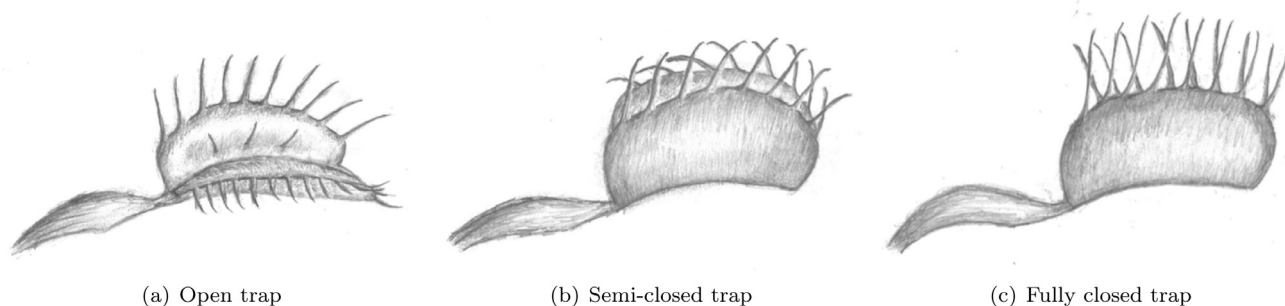


Fig. 1. A sketch of the three trap states of the Venus flytrap. Illustrations by the author, inspired by Darwin (1875, p.287).

cape, and retains only large prey. Darwin's idea has been well established, however it is rather difficult to observe prey escapes in nature as it may take more than twenty days for a prey to show up and cause the trap to close (Williams, 1980).
Thirdly, while the caught prey is struggling inside the trap, it will further stimulate the trigger hairs. This in turn will cause the lobes to tighten. Therefore, by struggling the caught prey will literally doom its fate. If the trap stops receiving further stimuli, presumably due to a prey escape or a false alarm, it will not advance to the fully closed state, but instead, slowly reverts back to the open state in about one day (Yang et al., 2010). Thus, if the caught prey knew better, it would remain still until an opportune time and walk away, as it were.

In the fully closed state the two lobes are held tightly together and curved inward, and the trap has essentially transformed into a stomach. The trap initiates the secretion of a digestive fluid, which first kills and then dissolves the prey (Scala et al., 1969). The trap assimilates nutrients from the prey, and slowly reduces the prey into a husk of chitin (Lichtner and Williams, 1977). After the trap has reopened, it will wait for some time for wind to blow away the remains of the prey, during which time it is insensitive to stimuli. It takes about two weeks for the trap to fully recover from handling a prey, after which the trap starts preying again (Yang et al., 2010).

Although the Venus flytrap has drawn great attention by botanists, there exists only few mathematical models about the plant. Recently, Yang et al. (2010) provided the first mathematical model to explain the closing and opening mechanism of a trap. The model was further advanced by Li et al. (2012), who showed through non-linear analysis that the open and fully closed states are stable, whereas the semi-closed state is unstable. Therefore, a semi-closed trap will reopen without any further energetic effort.

This paper is as much about providing the first mathematical cost-benefit model for carnivory in the Venus flytrap, as it is about understanding the ecology of the Venus flytrap. In particular, we bring Darwin's idea of allowing small prey to escape into a mathematical context. The purpose of this paper is to study the following questions about the Venus flytrap: How often does a trap capture and digest a prey? How often do non-prey sources such as raindrops or wind cause a trap to close? What are the costs and benefits of maintaining a large trap and allowing small prey to escape? To the best of the author's knowledge, there have been no previous attempts to answer these questions through mathematical modelling.

Since the process of capturing and digestion of prey in the Venus flytrap is rather complicated, we are faced with a dilemma: Although we wish to develop a rigorous mathematical model that captures every aspect of the process, the complexity of it makes this rather burdensome, if not impossible a task. Therefore, in order to gain an insight into the process, simplifications are inevitable. It is always up to the modeller to choose which fea-

tures are essential and, perhaps more importantly, which can be streamlined. A robust mathematical model requires a fine balance between abstractions and reality. Throughout the model development we aim to justify all of our abstractions, and make sure that they do not cause us to drift away from our quest; understanding the Venus flytrap.

The organisation of the paper is as follows. In Section 2 we separate the essential features from the irrelevant, in terms of our modelling purposes. We introduce a concept of trait, which consists of trap size and prey selection. The trait is inherent in every building block of the model, and becomes one of the main concepts of the paper. Then, a model describing the dynamics of prey capture is formulated as a system of ordinary differential equations. In Section 3 we derive the functional response of a trap of the Venus flytrap based on the individual behaviour. Then, in Section 4 we fit the model to available data and make various predictions regarding trap behaviour. In Section 5 we investigate the costs and benefits of carnivory in the Venus flytrap. We formulate an equation for the nutrient uptake per unit of time associated with carnivory. This allows us to compare the costs and benefits of different traits. Finally, in Section 6 we investigate optimisation of trap size and prey selection.

2. Dynamics of prey capture

Parameter	Description
β	Prey causes a trap to close
α	False alarm (e.g. raindrops or wind)
τ	Reopening time of a semi-closed trap
h	Prey handling time
p	Probability of prey escape

Let t and x denote time and the trait of a trap, respectively. By the trait x we understand a strategy that includes the physical trap size and size-based prey selection. The size of a trap can be measured as the length of the midrib connecting the two lobes. Similarly, the size of a prey can be measured by the length of its body. We assume that if a prey is larger than a trap, it does not cause the trap to close. This could be seen as a situation where the prey is too large to physically enter the trap. Alternatively, but to the same effect, one could think that when this large prey enters the trap, it bends multiple trigger hairs simultaneously. It has been shown that this may not result in closing of the trap (Brown and Sharp, 1910).

Following Darwin's (1875) hypothesis of allowing all small prey to escape from a trap, we assume that there is some threshold size x_1 for retaining a prey, otherwise it is allowed to escape. Let x_2 denote the physical size of a trap. Then, only the prey that have size between x_1 and x_2 are retained and digested. The trait

$x = (x_1, x_2)$ of a trap is thus 2-dimensional, and takes values in

$$x \in \{(x_1, x_2) \in \mathbb{R}^2 : 0 \leq x_1 < x_2\} := \Omega, \quad (1)$$

where Ω denotes the trait space. For each trait, the dynamics of prey capture are different, which also affect the costs and benefits of carnivory. These relationships are analysed in detail later in this research; for a graphical construction, see Fig. 4.

The trap is assumed to be characterised by its state and trait. We therefore introduce the density $n(x, t)$ for the traps with the trait x at time t , which are further divided into the three trap states: open and empty (n_o), semi-closed and empty (n_s), and fully closed with a prey item (n_h). Therefore,

$$n(x, t) = n_o(x, t) + n_s(x, t) + n_h(x, t). \quad (2)$$

For the sake of bookkeeping, we assume that prey escape occurs immediately after a small prey causes a trap to close. Let N describe the total density of all traps. Summing up over all possible traits one finds that the total trap density at time t is given by

$$N(t) = \int_{\Omega} n(x, t) dx. \quad (3)$$

If the resident population is monomorphic and consists of a single trait x , then $N(t) = n(x, t)$. For convenience, we often omit the term x from our notations.

We introduce the density R for the prey population. It is safe to assume that the effect of the Venus flytrap's predation is negligible on the prey population. Suppose that the prey is characterised only by its physical size, and that f describes the size distribution of the prey population. Then $\int_{x_1}^{x_2} f(\xi) d\xi$ is the fraction of prey with size between x_1 and x_2 . As of yet, we do not impose any particular conditions on the distribution f ; we merely assume that it is defined for $(0, \infty)$ as sizes are obviously positive quantities.

Let p describe the conditional probability that a prey escapes, or rather, is allowed to escape from a trap, given that it caused the trap to close. Then, using the size distribution f , we find that the probability of prey escape is described by

$$p = \frac{\int_0^{x_1} f(\xi) d\xi}{\int_0^{x_2} f(\xi) d\xi}. \quad (4)$$

Let β describe the per capita rate at which a prey causes a trap to close. Then, assuming that every prey in the size-interval $(0, x_2)$ is as likely to close a trap of size x_2 , we have

$$\beta = \beta_0 \int_0^{x_2} f(\xi) d\xi. \quad (5)$$

Here, the constant β_0 denotes the encounter rate with a prey of any size, while $\int_0^{x_2} f(\xi) d\xi$ describes the fraction of prey that cause the trap to close.

Let α describe the rate at which non-prey sources cause a trap to close. We assume a constant rate γ of trap closures by raindrops or wind, and a density dependent rate μN at which a trap causes another nearby trap to close. This implies that if the traps are dense, they are more likely to trip each other. Therefore, we have

$$\alpha = \gamma + \mu N. \quad (6)$$

The rate of transition from semi-closed to open state is a constant $1/\tau$, where τ is the average reopening time. Finally, the rate of transition from fully closed to open state is a constant $1/h$, where h is the average handling time.

With the assumptions mentioned above, we can write a system of ordinary differential equations for the short time scale dynamics of prey capture

$$\begin{aligned} \frac{d}{dt} n_o(t) &= -(\alpha + \beta R) n_o(t) + \frac{1}{\tau} n_s(t) + \frac{1}{h} n_h(t) \\ \frac{d}{dt} n_s(t) &= (\alpha + p\beta R) n_o(t) - \frac{1}{\tau} n_s(t) \\ \frac{d}{dt} n_h(t) &= (1-p)\beta R n_o(t) - \frac{1}{h} n_h(t). \end{aligned} \quad (7)$$

In particular,

$$\frac{d}{dt} n_o(t) + \frac{d}{dt} n_s(t) + \frac{d}{dt} n_h(t) = 0, \quad (8)$$

and so the density of the traps remains unchanged in the short time scale.

3. The Beddington–DeAngelis functional response

The functional response of a predator or, a trap in our context, is the number of prey a single predator consumes per unit of time. The well-known (Holling, 1959) type II functional response

$$G(R) = \frac{\beta R}{1 + \beta T R}, \quad (9)$$

where R denotes the prey population, is usually derived using a time-budgeting argument where the predators divide their time between searching for prey and handling the caught prey. Then, the parameters have clear-cut and biologically meaningful interpretations: β is the predation rate and T is the average handling time. Furthermore, the derivation by Holling (1959) showed that a predator spends a fraction $1/(1 + \beta T R)$ of its time searching, whereas the rest is spent handling. An alternative and more refined derivation by Metz and Diekmann (1986, pp. 6–7) is based on separating the short time scale of searching and handling prey from the long time scale of reproduction and dying. A generalisation to (9) has been proposed independently by Beddington (1975) and DeAngelis et al. (1975), namely

$$G(N, R) = \frac{a_1 R}{a_2 + a_3 N + a_4 R}. \quad (10)$$

The mathematical properties of Beddington–DeAngelis functional response (10) have been analysed since its proposal, such as determining the steady states, investigating their stability, and bifurcation of the parameters. Yet, biologically convincing mechanical derivations of (10) have long been lacking, and as such, the interpretations of the parameters a_i , for $i = 1, 2, 3, 4$, are often flawed. To our knowledge, there has been only one mechanistic derivation of (10) based on individual behaviour (Geritz and Gyllenberg, 2012). In particular, Geritz and Gyllenberg (2012) found that the term $a_3 N$ in the denominator of (10) reflects the behaviour of the prey. Moreover, they found that the parameter a_2 is in fact not a parameter at all, but a constant that could be fixed to 1. We now propose a new and simple mechanical derivation of the Beddington–DeAngelis functional response by the separation of time scales. Here, we find completely different biological interpretations for the terms a_2 and $a_3 N$.

In the previous section, we separated the short time scale of prey capture from the long time scale of reproduction and dying. Then, by setting the derivatives on the left-hand sides of (7) to equal zero and by using (2), one finds the equilibrium of the short time scale dynamics of prey capture

$$\begin{aligned} n_o &= \frac{n}{1 + \alpha \tau + \beta(p\tau + (1-p)h)R} \\ n_s &= \frac{(\alpha + p\beta R)\tau n}{1 + \alpha \tau + \beta(p\tau + (1-p)h)R} \\ n_h &= \frac{(1-p)h\beta R n}{1 + \alpha \tau + \beta(p\tau + (1-p)h)R}. \end{aligned} \quad (11)$$

Now, as $(1-p)\beta$ is the rate of capturing and retaining a prey, and a trap is open a fraction n_o/n of its time, we find that the number of prey consumed by a single trap per unit of time is:

$$(1-p)\beta R \frac{n_o}{n} = \frac{(1-p)\beta R}{1 + \alpha\tau + \beta(p\tau + (1-p)h)R} = G(N, R), \quad (12)$$

where G is the functional response of a trap of the Venus flytrap. We have thus derived the functional response based on assumptions made about individual behaviour. Furthermore, by rewriting G with the explicit expression of α and

$$\begin{aligned} a_1 &= (1-p)\beta \\ a_2 &= 1 + \gamma\tau \\ a_3 &= \mu\tau \\ a_4 &= \beta(p\tau + (1-p)h), \end{aligned} \quad (13)$$

we have arrived at the Beddington–DeAngelis functional response (10). Moreover, we have found that the terms α_i , $i = 1, 2, 3, 4$, all describe trap behaviour. One could argue that the escape probability p is actually part of the prey behaviour. However, it was assumed that it is always the size of the prey that determines the outcome of the struggle. A moderately large prey can never escape, whereas a small prey always escapes. Therefore, a prey cannot affect the outcome of the struggle by its own behaviour.

If we had originally merely assumed that a trap of the Venus flytrap has the Beddington–DeAngelis functional response, it would have been near impossible to arrive at convincing interpretation of the parameters. This underlines the importance of a mechanical derivation of the functional response. If $\mu = 0$, then G reduces to the Holling type II functional response. Therefore, the assumption that in tight clusters other traps may be a potential source for trap closures was the fundamental part of trap behaviour that led to this result.

In the same spirit of the above derivation of the functional response, we can also investigate the trap closures per unit of time. Since $\alpha + \beta R$ is the rate of transition from open to closed state, and a trap is open a fraction n_o/n of its time, then the average number of trap closures per unit of time for a single trap is

$$(\alpha + \beta R) \frac{n_o}{n} = \frac{\alpha + \beta R}{1 + \alpha\tau + \beta(p\tau + (1-p)h)R} = H(N, R). \quad (14)$$

Moreover, by using (12), H can be written in terms of G ,

$$H(N, R) = \frac{\alpha + \beta R}{(1-p)\beta R} G(N, R). \quad (15)$$

4. Analysis of trap closures

There exists little field data about prey escapes and trap closures in the Venus flytrap (Williams, 1980). It is not known how often raindrops or wind causes a trap to close. This could be because it can be difficult to observe trap closures in nature as it may take more than twenty days until a prey shows up and causes a trap to close (Williams, 1980). It can also be rather difficult to adequately study hypothetical size-based prey selection in nature, as one would have to implement a method for capturing the prey that were allowed to escape from traps of the Venus flytrap. The equilibrium of the trap states and reopening times, on the other hand, can be easier to estimate. Assume that the equilibrium state of the dynamics of prey capture (7) is known. Recall that p is the probability that a prey escapes from a trap. By solving p from (11), we find that

$$p = \frac{1 - \alpha\tau \frac{n_o}{n_s}}{1 + \frac{\tau}{h} \frac{n_h}{n_s} - \alpha\tau \frac{n_o}{n_s}}. \quad (16)$$

Conversely, by solving the rates of trap closure α and βR from (11), we find that

$$\alpha = \frac{1}{\tau} \frac{n_s}{n_o} - \frac{p}{(1-p)h} \frac{n_h}{n_o}, \quad (17)$$

$$\beta R = \frac{n_h}{(1-p)hn_o}. \quad (18)$$

By using the above expressions for α and βR , we can obtain more information about trap closures. The proportion of trap closures caused by false alarms is simply

$$\frac{\alpha}{\alpha + \beta R} = \frac{1 - \frac{\tau}{h} \frac{p}{1-p} \frac{n_h}{n_s}}{1 + \frac{\tau}{h} \frac{n_h}{n_s}}. \quad (19)$$

Since a fraction $1-p$ of the caught prey are retained, the probability that a trap closure results in a meal is

$$\frac{(1-p)\beta R}{\alpha + \beta R} = \frac{1}{1 + \frac{h}{\tau} \frac{n_s}{n_h}}. \quad (20)$$

We also observe that since $\alpha + \beta R$ is the total rate of transition from open to closed state, then the average time until an open trap snaps shut is given by

$$\frac{1}{\alpha + \beta R} = \frac{n_o}{n_s/\tau + n_h/h}. \quad (21)$$

Now, by collecting the above information we can solve the average time until a trap finds a meal. At first a trap is open, waiting for something to cause it to close. After an average time (21) the trap snaps shut, and this leads to a meal with probability (20), otherwise the closure is wasted. After false alarm or small prey escape, the trap reopens in an average time τ . This process is iterated until the trap finally captures a large prey that leads to a meal. Obviously, these consecutive trap closures are independent events. Thus, the average time a trap has to wait for a meal is given by

$$\begin{aligned} & \frac{(1-p)\beta R}{\alpha + \beta R} \frac{1}{\alpha + \beta R} + \frac{\alpha + p\beta R}{\alpha + \beta R} \frac{(1-p)\beta R}{\alpha + \beta R} \left(\frac{2}{\alpha + \beta R} + \tau \right) \\ & + \left(\frac{\alpha + p\beta R}{\alpha + \beta R} \right)^2 \frac{(1-p)\beta R}{\alpha + \beta R} \left(\frac{3}{\alpha + \beta R} + 2\tau \right) + \dots \\ & = \frac{(1-p)\beta R}{\alpha + \beta R} \sum_{n=0}^{\infty} \left(\frac{\alpha + p\beta R}{\alpha + \beta R} \right)^n \left(\frac{n+1}{\alpha + \beta R} + n\tau \right) \\ & = \frac{1}{\alpha + \beta R} \left(1 + (1 + \tau(\alpha + \beta R)) \frac{\alpha + p\beta R}{(1-p)\beta R} \right) \\ & = \frac{n_o}{n_s/\tau + n_h/h} \left(1 + \left(1 + \frac{n_s}{n_h} + \frac{\tau}{h} \frac{n_h}{n_o} \right) \frac{h}{\tau} \frac{n_s}{n_h} \right), \end{aligned} \quad (22)$$

where in the last step we applied the explicit expressions (17) and (18) for α and βR .

We now apply the available data to better understand these observations. Hutchens and Luken (2009) collected a relatively large sample of 861 traps, and divided them into three size classes. Here, the results for the largest size class are applied. It was estimated that the fractions of open traps, semi-closed and empty traps, and fully closed traps with a prey item were given by

$$n_o/n = 0.536, \quad n_s/n = 0.233, \quad n_h/n = 0.231. \quad (23)$$

Among the research papers about the Venus flytrap, there exists a number of estimates for the trap reopening and handling times (Darwin, 1875; Lloyd, 1942; Scala et al., 1969; Lichtner and Williams, 1977; Gibson and Waller, 2009; Yang et al., 2010). Reopening a semi-closed trap takes about 8–24 h, and handling a prey takes about one to two weeks.

In Figs. 2 and 3 we, have plotted the equations (16) and (19) for different estimates on the reopening and handling times. These figures suggest that unless the probability of prey escape is very high

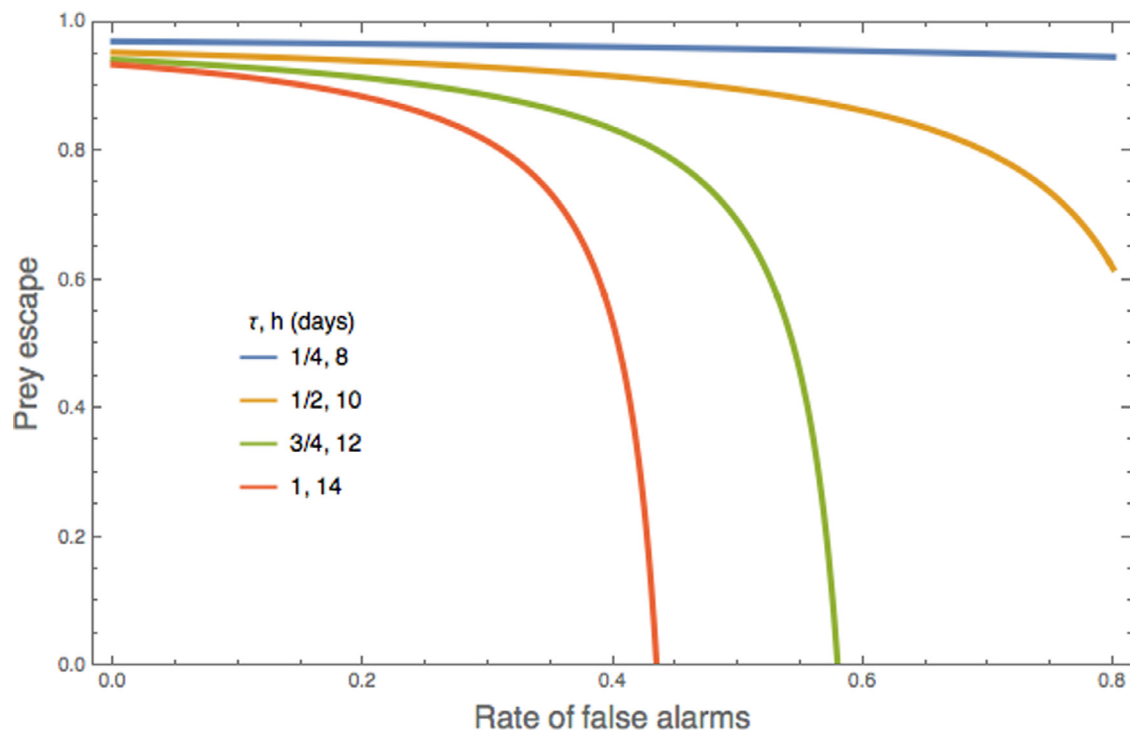


Fig. 2. Relationship of small prey escape and false alarms.

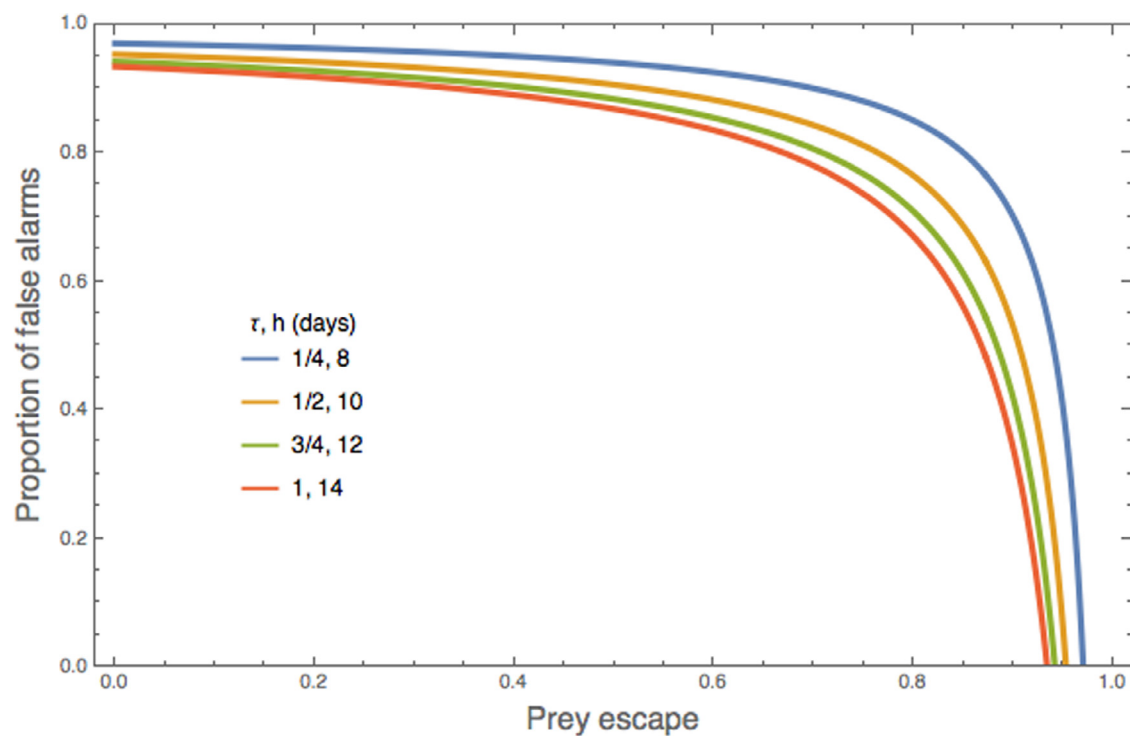


Fig. 3. Relationship of small prey escape and proportion of false alarms. This suggests that a large proportion of trap closures are false alarms, which are caused by non-prey sources such as raindrops or wind.

(> 90%), then a large proportion of trap closures are caused by non-prey sources. Next, we apply these estimates on the equations (21) and (22). This results in that the time until a trap closure takes place is 1–2 days, and that the average time a trap has to wait for a meal is 26–46 days. The probability that a trap closure results in a meal is 3–6.6%. As such, these predictions indicate that a trap has to wait a long time for a meal; non-prey sources, such as

raindrops or wind, cause a large proportion of trap closures; and only few trap closures result in a meal.

5. Costs and benefits of carnivory

The marshy soil in which the Venus flytrap can be found is abundant both in moisture and light, but the nitrogen and

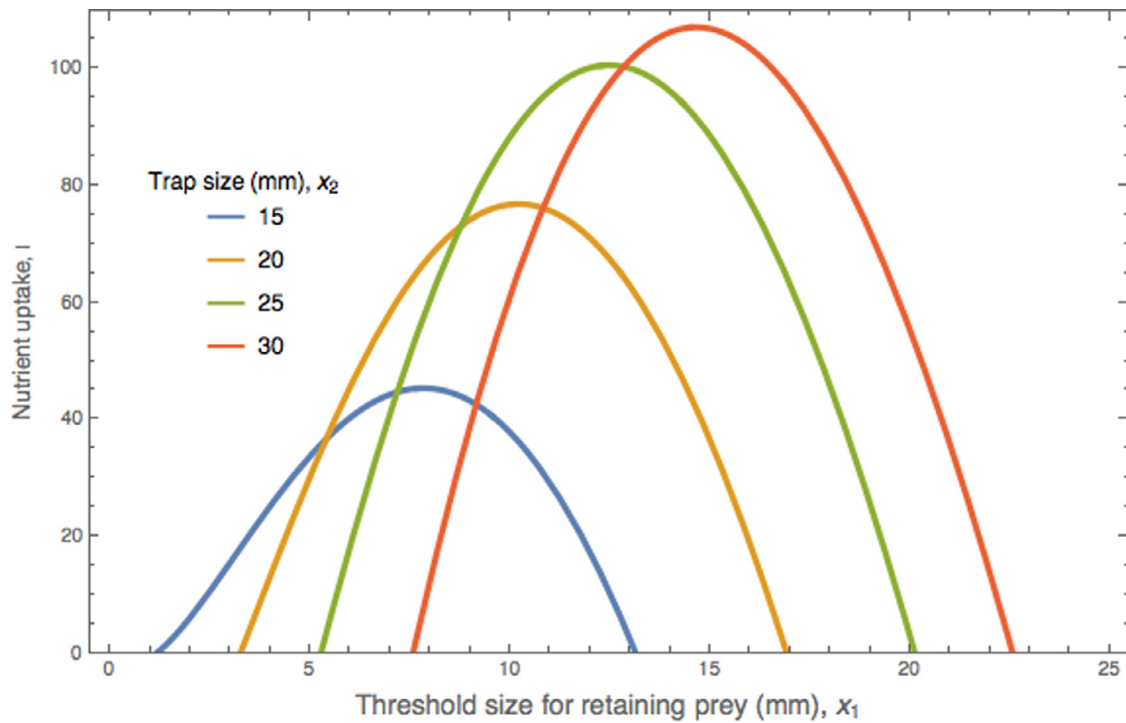


Fig. 4. Graphical construction of nutrient uptake for different traits. For each trap size, there exists an optimal threshold for retaining prey. If prey selection remains unchanged as a trap increases in size, then the nutrient uptake decreases. This illustrates how the traps become more selective as they grow in size.

phosphorus concentrations are scarce. Therefore, the plant has evolved to compensate for the poor soil by capturing and digesting prey with snap-traps (Givnish et al., 1984; Ellison, 2006). The process of handling a prey presumably has a high cost (Ellison, 2006). If the digested prey is too small, it is likely that the cost will exceed the gain, which results in a disadvantageous meal. Moreover, the whole process of handling a prey can take two weeks to complete (Yang et al., 2010). Thus, it may not be worthwhile to go through the digestion even if there is a marginal profit, because of the many days wasted in remaining closed.

Let E describe the average size of a consumed prey for a trap with the trait $x = (x_1, x_2)$,

$$E = \frac{\int_{x_1}^{x_2} \xi f(\xi) d\xi}{\int_{x_1}^{x_2} f(\xi) d\xi}. \quad (24)$$

Following the results of Gibson and Waller (2009), we assume that the size distribution f of prey is log normally distributed, with mean 2.1996 and standard deviation 0.9578. To the best of the author's knowledge, there has been no other attempts to estimate the size distribution. The biomass B of a prey is assumed to be described as a function of prey size,

$$B(l) = B_0 \cdot l^b, \quad (25)$$

where we set $B_0 = 10^{-1.297}$ and $b = 2.6463$ as in Gibson and Waller (2009). (The author was kindly informed by Waller that $B_0 = 10^{-1.297}$.) We assume that the nutrient uptake via prey digestion is proportional to the biomass of the prey with a constant conversion efficiency λ . This would indicate that every trap is equally efficient in absorbing nutrients from prey.

Let C and D , respectively, denote the energetic costs of a trap closure and digestion in terms of nutrients. For C , we choose

$$C = c\lambda B(x_2), \quad \text{where } c \in (0, 1), \quad (26)$$

and for D , we choose

$$D = d\lambda B(x_2), \quad \text{where } d \in (0, 1). \quad (27)$$

Therefore, we assume that each cost can be described as a fraction of the nutrient gain from the largest feasible prey. These choices on C and D provide us a straightforward method for fitting the model to the data by fine tuning c and d .

By combining the costs and benefits of carnivory, and the number of prey consumed by a trap per unit of time, we can write nutrient uptake per unit of time I associated with carnivory,

$$\begin{aligned} I &= \frac{\text{Prey caught}}{\text{Unit of time}} \cdot (\text{Benefit} - \text{Cost of digestion}) \\ &\quad - \frac{\text{Trap closures}}{\text{Unit of time}} \cdot \text{Cost of closure} \\ &= G(N, R) \cdot (\lambda B(E) - D) - H(N, R) \cdot C. \end{aligned} \quad (28)$$

As we rewrite H with the expression given by (15),

$$I = G(N, R) \cdot \left(\lambda B(E) - D - C \frac{\alpha + \beta R}{(1 - p)\beta R} \right), \quad (29)$$

then it becomes clear that I is a product of two components with clear-cut biological interpretations. The functional response G describes the number of prey consumed by a single trap per unit of time; whereas the expression inside the brackets in (29) is the net return per consumed prey. In particular, this expression contains the average cost that a trap has to pay for each meal. This does not only include the process of digestion, but also all the ineffectual trap closures before an actual meal.

In Fig. 4 the nutrient uptake I has been plotted for different trap sizes. This illustrates how a larger trap have potential for higher nutrient uptake. However, in order to achieve those high uptakes the large trap must allow small prey to escape. For example, with a trap size of 30 mm, all prey smaller than about 15 mm should be allowed to escape in order to maximise the nutrient uptake. Moreover, if a trap digests prey smaller than 8 mm, then the nutrient uptake becomes negative: the costs exceed the benefits. This suggests that a trap cannot survive unless it allows small prey to

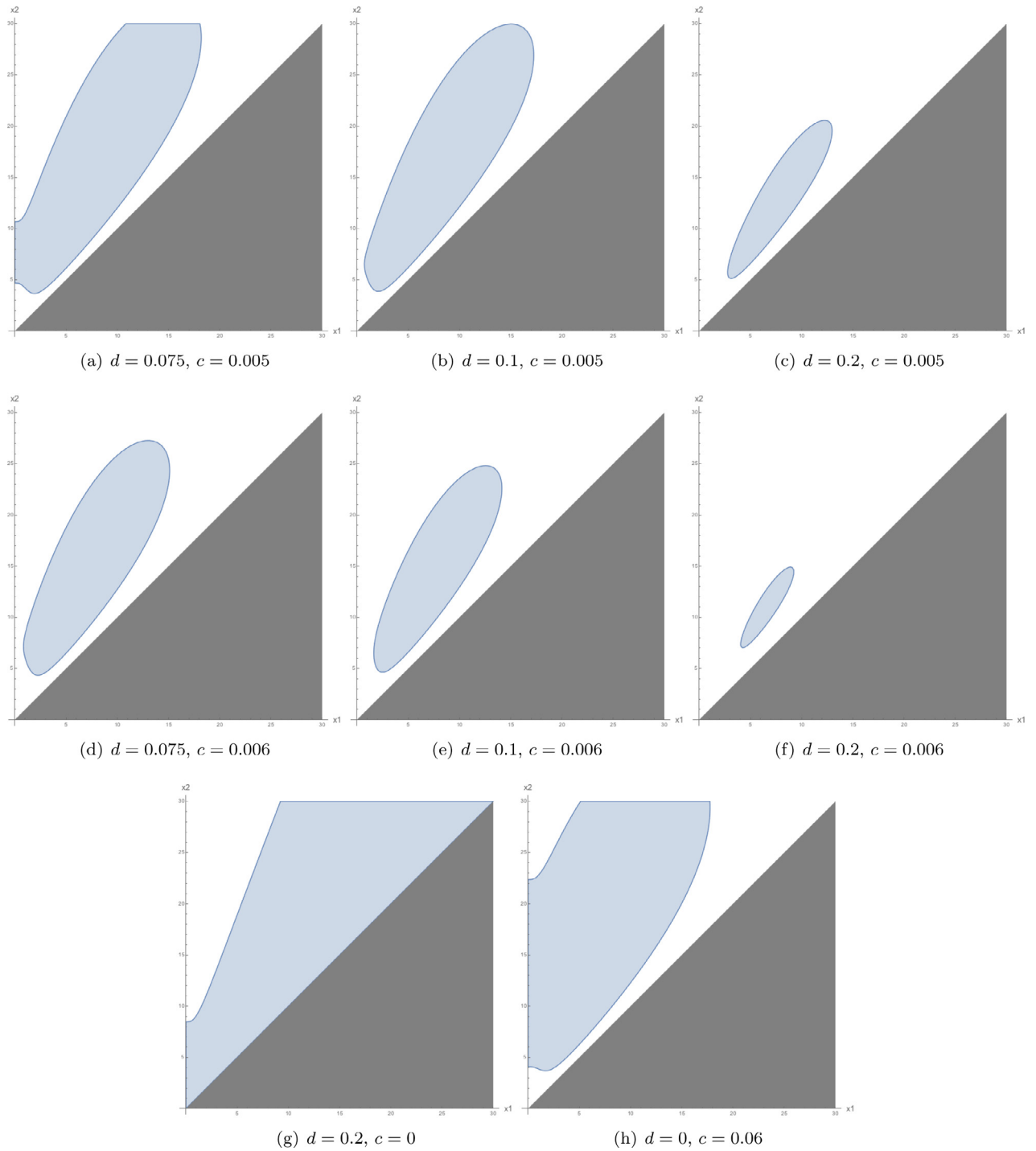


Fig. 5. Graphical construction of the region of viable traits Ω_0 for different costs of trap closure and digestion. All panels show the region Ω_0 in blue. Panels (a) to (f) illustrate how the region Ω_0 diminishes as the costs increase. Note that Ω_0 is bounded and connected. Panel (g) shows the special case where trap closure has no cost. This results in an unbounded Ω_0 , which would essentially mean that trap size is not constrained by ecological factors. Finally, panel (h) shows the special case where digestion has no cost. This would mean that even a large trap does not need to be selective at all to sustain positive nutrient uptake. These panels illustrate how the costs of trap closure and digestion constrain trap size and prey selection. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

escape. A similar outcome also occurs if the trap is too selective on its prey and retains only the prey of a size larger than 22 mm.

The necessary but not sufficient condition for viability requires that $I > 0$, that is,

$$\lambda B(E) - D - C \frac{\alpha + \beta R}{(1-p)\beta R} > 0. \quad (30)$$

Let Ω_0 describe the region of all traits resulting in a positive nutrient uptake,

$$\Omega_0 = \{x \in \Omega : I(x) > 0\}. \quad (31)$$

It is only within this region where carnivory is favourable for the Venus flytrap; for every trait outside this region the costs exceed

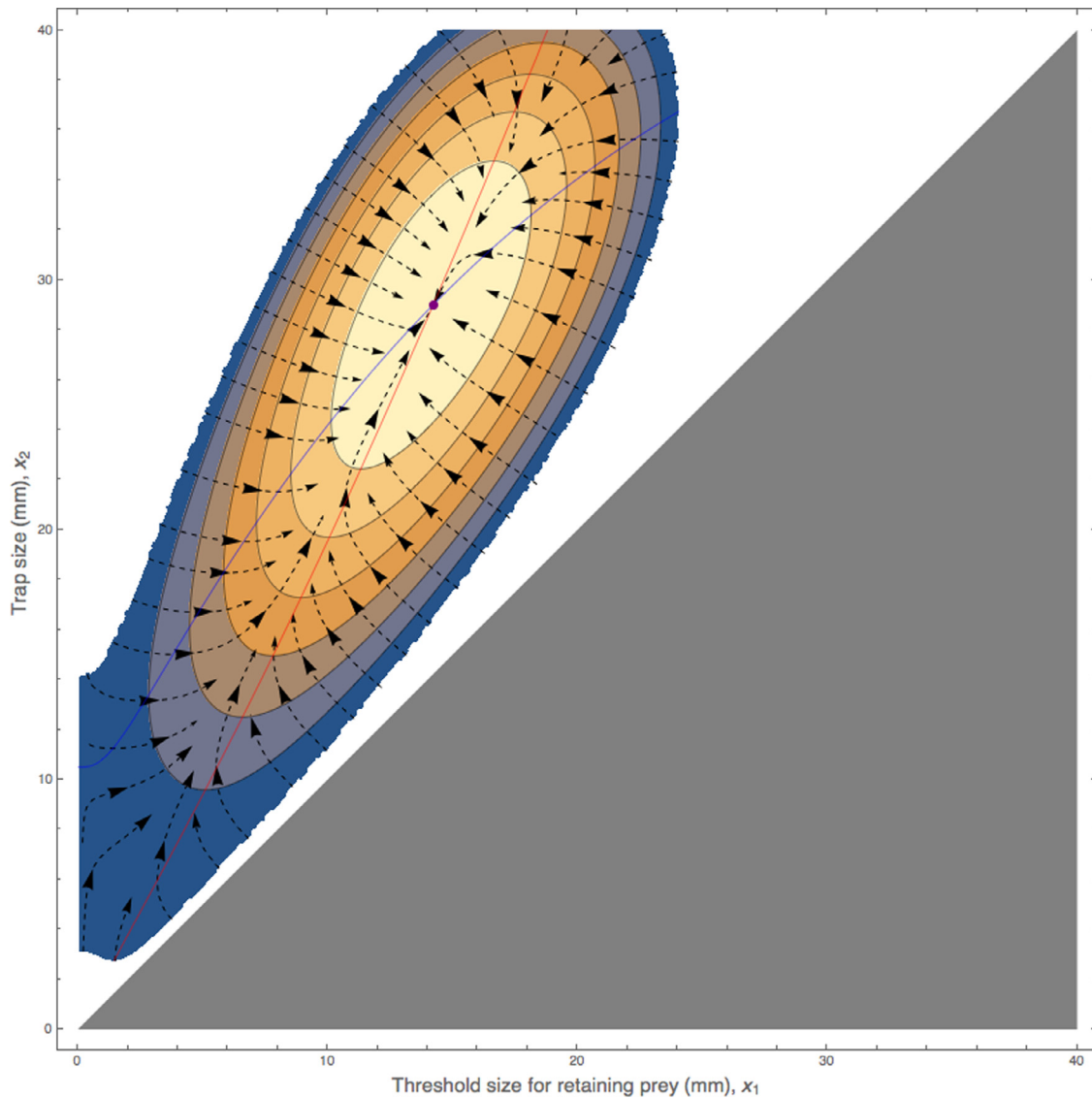


Fig. 6. Graphical construction of the optimisation process of trap size and prey selection for hypothetical parameters. Contours of the region Ω_0 are shown in colours. The vector field $W'_x(y)|_{y=x}$ is shown in dashed arrows, and the isoclines are shown as red and blue curves for x_1 and x_2 , respectively. At the intersection of the isoclines we have the optimal trait x^* . In this hypothetical situation $x^* \approx (14.2, 29)$, that is, a trap allows all prey smaller than 14.2 mm to escape, and the trap size is 29 mm. The results are for f log normal distributed (mean 2.1996, SD 0.9578) and for parameter values $\alpha = 0.0275$, $\beta_0 = 0.004$, $R = 1$, $\tau = 12$, $h = 240$, $b = 2.6463$, $c = 0.005$ and $d = 0.075$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the gains. By using the explicit expressions for B , C and D , we can rewrite Ω_0 as

$$\Omega_0 = \left\{ x \in \Omega : E(x)^b - \left(d + c \frac{\alpha + \beta R}{(1-p)\beta R} \right) x_2^b > 0 \right\}. \quad (32)$$

In particular, the condition for viability is independent of the positive constant term λB_0 . In Fig. 5 the region Ω_0 has been graphically constructed for hypothetical parameter values.

6. Optimisation of trap size and prey selection

In the Venus flytrap, a plant that is native to such harsh conditions, optimising the costs and benefits of carnivory is absolutely essential. A plant whose traps yields better nutrient uptake than the conspecific, is likely to be competitively superior. A greater nutrient uptake is likely to result in a larger number of seeds produced per plant, and to also increase the survivability of a plant. We assume that the nutrient uptake associated with carnivory describes the fitness of a trap. In reality, there are many other ecological factors that contribute to the fitness of a trap. Therefore, we

cannot make strong statements about the optimisation process, but rather, give an explanation as to why certain trap sizes are more likely to be observed in nature.

Consider two nearby traits x and y . Whether y is competitively superior to x or not has to be determined from the sign of $I(y) - I(x)$. By using all the information collected throughout the paper, we find that this can be done by investigating the following function

$$W_x(y) = \tilde{G}_y[E(y)^b - Q_y y_2^b] - \tilde{G}_x[E(x)^b - Q_x x_2^b]. \quad (33)$$

In (33) we have employed the following notation.

$$\begin{aligned} \tilde{G}_x &= \frac{\int_{x_1}^{x_2} f(\xi) d\xi}{1 + \alpha\tau + \beta_0 R (\tau \int_0^{x_1} f(\xi) d\xi + h \int_{x_1}^{x_2} f(\xi) d\xi)}, \\ Q_x &= d + c \frac{\alpha + \beta_0 R \int_0^{x_2} f(\xi) d\xi}{\beta_0 R \int_{x_1}^{x_2} f(\xi) d\xi}. \end{aligned} \quad (34)$$

Since we have mechanically derived every single term in $W_x(y)$ from the individual behaviour, their interpretations are clear-cut and biologically meaningful. If $W_x(y) > 0$, then the trait y yields

higher nutrient uptake per unit of time that the trait x . However, the explicit expression of $W_x(y)$ is awfully complicated, which makes any purely mathematical analysis rather difficult.

The optimisation process is thus an uphill climb towards higher nutrient uptake values, and the direction is described by the following gradient

$$W'_x(y)|_{y=x} = \left(\frac{\partial W_x(y)}{\partial y_1}, \frac{\partial W_x(y)}{\partial y_2} \right) \Big|_{y=x}. \quad (35)$$

Any optimal trait x^* has to locate on a peak, where no nearby traits can yield higher nutrient uptake. Therefore, a trait x^* is optimal if and only if it satisfies the following conditions

$$\begin{aligned} W'_x(y)|_{y=x^*} &= (0, 0), \\ \frac{\partial^2 W_x(y)}{\partial y_1^2} \Big|_{y=x^*} &< 0, \\ \frac{\partial^2 W_x(y)}{\partial y_2^2} \Big|_{y=x^*} &< 0, \\ \left[\frac{\partial^2 W_x(y)}{\partial y_1^2} \frac{\partial^2 W_x(y)}{\partial y_2^2} - \frac{\partial W_x(y)}{\partial y_1} \frac{\partial W_x(y)}{\partial y_2} \right] \Big|_{y=x^*} &> 0. \end{aligned} \quad (36)$$

In Fig. 6 this process of optimising the trait has been plotted for a hypothetical set of parameters. In this particular example the optimal trait is $x^* \approx (14.2, 29)$. Therefore, a trap with the trait x^* maximises nutrient uptake, which is the perfect balance between physical trap size (29 mm) and prey selection by allowing small prey (< 14.2 mm) to escape.

In this example we chose the model parameters to fit the data collected by Gibson and Waller (2009), which suggested that for an optimal trap the average size of digested prey is 20 mm. Now, we have showed that this optimal trap has size 29 mm, and allows prey smaller than 14.2 mm to escape. Although the average meal is only about 68.9% of the maximum potential of the trap, the potential to capture large prey rewards the trap with occasional energetic ‘jackpots’, as they were. This is because the prey biomass scales as a power function of size. Moreover, it is a surprisingly large proportion 76.8% of the captured prey that are allowed to escape, implying that the Venus flytrap is highly selective in its prey capture.

7. Main results

Investigating the costs and benefits of carnivory in the Venus flytrap is important to understanding the ecology of the plant. These factors posit a trade-off between investments in the snap-trap structures and potential energetic benefits associated with carnivory. In addition to this trade-off, the complex snap-trap structure provides the Venus flytrap with the unique ability to allow small prey to escape, and wait until a moderately large prey has been captured. It can be difficult to understand these relations without a mathematical model.

In this paper we have provided the first mathematical cost-benefit model for carnivory in the Venus flytrap, which has allowed us to investigate these trade-offs. By fitting the model to the available data, we have been able to make various experimentally observable predictions regarding trap behaviour. We have predicted that non-prey sources, such as raindrops or wind, cause a large proportion of trap closures while only few ($< 6.6\%$) result in a meal; the closure mechanism of a trap is triggered about once every two days; and a trap has to wait more than a month for a meal.

The cost-benefit model has allowed us to clearly illustrate how a large trap yields high nutrient uptake if it also allows small prey to escape. To some extent, even small traps are selective in their

prey capture. Through a concrete example, we have showed how the trap finds the optimal balance between the physical trap size of 29 mm and allowing small prey with size less than 14.2 mm to escape. For a optimal trap, the average size of a digested prey is 20 mm, which means that on average the trap utilises 68.9% of its maximum potential. Although the sizes of many of the consumed prey are well below the maximum capacity of the trap, the potential to capture large prey rewards the trap with occasional peaks in terms of energetic benefits. Moreover, we have showed that the optimal trap allows 76.8% of the captured prey to escape. These predictions indicate that the Venus flytrap is highly selective in its prey capture.

By analysing the dynamics of prey capture, we have also found a new mechanistic derivation of the Beddington–DeAngelis functional response. The mechanistic derivation has provided clear-cut and biologically meaningful interpretations of the parameters, and has showed an example where every parameter in the functional response is part of the Venus flytrap behaviour, while none of them represent the prey behaviour. This finding underlines the importance of the mechanistic derivation of the functional response.

8. Conclusion

The ecology of the Venus flytrap is by far one of the least understood aspects of the plant, which is why investigating capturing and digestion of prey is important. This paper provides the first building blocks for modelling the ecology of the Venus flytrap. The next natural step is to extend our model for the long time scale dynamics of reproduction and dying, which could incorporate the various growth stages of a trap. This would make it possible to investigate many other interesting aspects of the plant, such as the average number of traps per plant, and the costs and benefits associated with the growth of a trap.

It is known that the traps start their life small, and the amount of growth is related to the prosperity of their prey capture (Hatcher and Hart, 2014). Therefore, the traps provide initially only little nutriment to the plant, as is suggested by Fig. 4. But since the plant is highly adaptive to its habitat, the traps grow quickly in size to increase their nutrient uptake. On the other hand, high adaptation also means that only few traps reach the optimal size, as this would require capturing the right sized insects. This implies that there will be wide variance in trap sizes, which is in agreement with the experimental data (Hutchens and Luken, 2009). However, it is unlikely that the growth would come to a halt at the optimum, and so a trap that is able to capture many insects during its life would eventually grow too large to be efficient. This raises the issue of when a trap should senesce.

In the present paper we have studied only the costs and benefits of prey capturing, but it should be noted that the ecological context of the Venus flytrap is far more complicated. For example, it has been suggested that occasional fires in the habitat may enhance the plant's growth rate (Schulze et al., 2001).

Most often the difficulties in our research had to do with the lack of available data about the Venus flytrap and its prey. This has forced us to simplify its behaviour to make up for the missing pieces of the puzzle, as it were. To overcome these obstacles, and to further advance our understanding of the plant, we should seek to collect more data in the endemic habitat of the Venus flytrap.

Acknowledgements

I thank Mats Gyllenberg for comments on previous drafts of this paper. This research was funded by the Academy of Finland, Centre of Excellence in Analysis and Dynamics Research.

References

- Beddington, J., 1975. Mutual interference between parasites or predators and its effect on searching efficiency. *J. Anim. Ecol.* 44, 331–340. doi:[10.2307/3866](https://doi.org/10.2307/3866).
- Brown, W., Sharp, L., 1910. The closing response in *Dionaea*. *Bot. Gazette* 49 (4), 290–302. doi:[10.1086/330177](https://doi.org/10.1086/330177).
- Darwin, C., 1875. *Insectivorous Plants*. John Murray.
- DeAngelis, D., Goldstein, R., O'Neill, R., 1975. A model for trophic interaction. *Ecology* 56 (4), 881–892. doi:[10.2307/1936298](https://doi.org/10.2307/1936298).
- Ellison, A., 2006. Nutrient limitation and stoichiometry of carnivorous plants. *Plant Biol.* 8 (6), 740–747. doi:[10.1055/s-2006-923956](https://doi.org/10.1055/s-2006-923956).
- Ellison, A., Gotelli, N., 2001. Evolutionary ecology of carnivorous plants. *Trends Ecol. Evol.* 16 (11), 623–629. doi:[10.1016/S0169-5347\(01\)02269-8](https://doi.org/10.1016/S0169-5347(01)02269-8).
- Ellison, A., Gotelli, N., 2009. Energetics and the evolution of carnivorous plants—Darwin's 'most wonderful plants in the world'. *J. Exp. Bot.* 60 (1), 19–42. doi:[10.1093/jxb/ern179](https://doi.org/10.1093/jxb/ern179).
- Forterre, Y., Skotheim, J., Dumais, J., Mahadevan, L., 2005. How the Venus flytrap snaps. *Nature* 433, 421–425. doi:[10.1038/nature03185](https://doi.org/10.1038/nature03185).
- Geritz, S., Gyllenberg, M., 2012. A mechanistic derivation of the DeAngelis–Beddington functional response. *J. Theor. Biol.* 314, 106–108. doi:[10.1016/j.jtbi.2012.08.030](https://doi.org/10.1016/j.jtbi.2012.08.030).
- Gibson, T., Waller, D., 2009. Evolving Darwin's 'most wonderful' plant: ecological steps to a snap-trap. *New Phytol.* 183 (3), 575–587. doi:[10.1111/j.1469-8137.2009.02935.x](https://doi.org/10.1111/j.1469-8137.2009.02935.x).
- Givnish, T., Burkhardt, E., Happel, R., Weintraub, J., 1984. Carnivory in the Bromeliad *Brocchinia reducta*, with a cost/benefit model for the general restriction of carnivorous plants to sunny, moist, nutrient-poor habitats. *Am. Nat.* 124 (4), 479–497. doi:[10.1086/284289](https://doi.org/10.1086/284289).
- Hatcher, C., Hart, A., 2014. Venus flytrap seedlings show growth-related prey size specificity. *Int. J. Ecol.* 2014. doi:[10.1155/2014/135207](https://doi.org/10.1155/2014/135207).
- Hodick, D., Sievers, A., 1989. On the mechanism of trap closure of Venus flytrap (*Dionaea muscipula* Ellis). *Planta* 179 (1), 32–42. doi:[10.1007/BF00395768](https://doi.org/10.1007/BF00395768).
- Holling, C., 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91 (7), 385–398. doi:[10.4039/Ent91385-7](https://doi.org/10.4039/Ent91385-7).
- Hutchens, J., Luken, J., 2009. Prey capture in the Venus flytrap: collection or selection? *Botany* 87 (10), 1007–1010. doi:[10.1139/B09-064](https://doi.org/10.1139/B09-064).
- Kruse, J., Gao, P., Honsel, A., Kreuzwieser, J., Burzlaff, T., Alfarraj, S., Hedrich, R., Rennenberg, H., 2014. Strategy of nitrogen acquisition and utilization by carnivorous *Dionaea muscipula*. *Oecologia* 174 (3), 839–851. doi:[10.1007/s00442-013-2802-9](https://doi.org/10.1007/s00442-013-2802-9).
- Li, Y., Lenaghan, S., Zhang, M., 2012. Nonlinear dynamics of the movement of the Venus flytrap. *Bull. Math. Biol.* 74 (10), 2446–2473. doi:[10.1007/s11538-012-9760-y](https://doi.org/10.1007/s11538-012-9760-y).
- Lichtner, F., Williams, S., 1977. Prey capture and factors controlling trap narrowing in *Dionaea* (Droseraceae). *Am. J. Bot.* 64 (7), 881–886.
- Lloyd, F.E., 1942. *The Carnivorous Plants*. A New Series of Plant Science Books, 9, first ed. Chronica Botanica Company, Waltham.
- Metz, J., Diekmann, O., 1986. *The Dynamics of Physiologically Structured Populations*. Lecture Notes in Biomathematics, 68, first ed. Springer-Verlag, Berlin.
- Pavlovič, A., Saganová, M., 2015. A novel insight into the cost–benefit model for the evolution of botanical carnivory. *Ann. Bot.* 115 (7), 1075–1092. doi:[10.1093/aob/mcv050](https://doi.org/10.1093/aob/mcv050).
- Scala, J., Iott, K., Schwab, D., Semersky, F., 1969. Digestive secretion of *Dionaea muscipula* (Venus's-flytrap). *Plant Physiol.* 44 (3), 367–371. doi:[10.1104/pp.44.3.367](https://doi.org/10.1104/pp.44.3.367).
- Schulze, W., Schulze, E., Schulze, I., Oren, R., 2001. Quantification of insect nitrogen utilization by the Venus fly trap *Dionaea muscipula* catching prey with highly variable isotope signatures. *J. Exp. Bot.* 52 (358), 1041–1049. doi:[10.1093/jexbot/52.358.1041](https://doi.org/10.1093/jexbot/52.358.1041).
- Volkov, A., Adesina, T., Markin, V., Jovanov, E., 2008. Kinetics and mechanism of *Dionaea muscipula* trap closing. *Plant Physiol.* 146 (2), 694–702. doi:[10.1104/pp.107.108241](https://doi.org/10.1104/pp.107.108241).
- Williams, S., 1980. How Venus flytraps catch spiders and ants. *Carnivorous Plant Newsl.* 9, 65–78.
- Yang, R., Lenaghan, S., Zhang, M., Xia, L., 2010. A mathematical model on the closing and opening mechanisms for Venus flytrap. *Plant Signaling Behav.* 5 (8), 968–978. doi:[10.4161/psb.5.8.12136](https://doi.org/10.4161/psb.5.8.12136).